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BIOLOGICAL BULLETIN

ECOLOGICAL SUCCESSION.

II. POND FISHES.

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I. INTRODUCTION.

In the first paper of this series ("Stream Fishes and Physiographic Analysis"), we pointed out the reasons for undertaking this investigation and stated the purposes around which the work has centered. There we were concerned with the value of the principles of physiography in a method of locating the animal in the environment and of determining something of its character as a whole. Here we are to discuss the value of plant succession in a similar way and to have a better opportunity to show the validity of the principle of succession as applied to animals. Furthermore, as we pointed out in the other paper, ecological succession is to be differentiated from geological suc-

cession. Ecological succession is succession of ecological types regardless of species, while geological succession is the succession of species. The data presented here affords an excellent opportunity to bring out the differences and relations of these two types of succession.

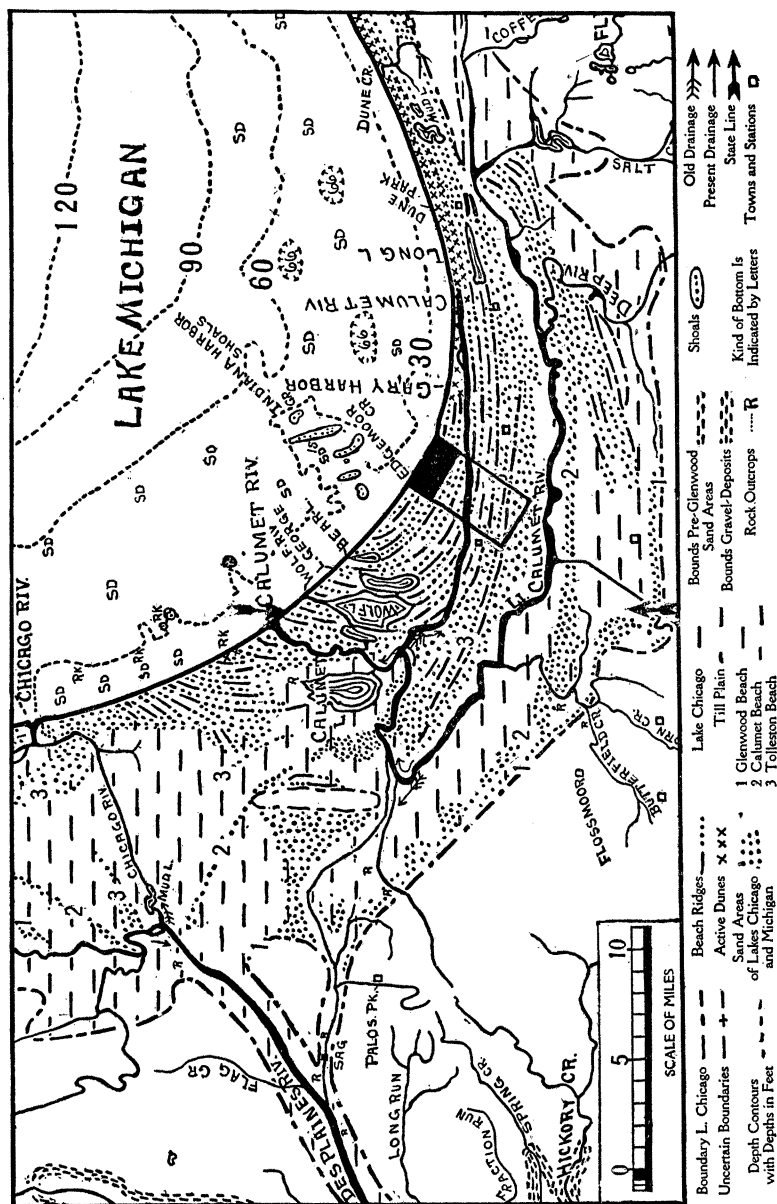
We noted also in the first paper that the first recognition of plant and animal succession came with the development of genetic physiography. It was mainly the succession which accompanies physiographic change. Cowles ('01) also clearly recognized succession due to the action of plants themselves. This latter idea has been elaborated by Clements ('05) and essentially demonstrated by Schantz ('06) and Dacknowski ('08). Animals must obviously play an important rôle in this type of succession, but unfortunately this has not been investigated.

The succession with which we will deal in this paper is that resulting from the action of organisms on their own environment. For all practical purposes the area selected for this study has been in a condition of physiographic stability for a considerable period. The selection and analysis of the place of study is the most important step in the whole investigation. Indeed there are only a few suitable localities in North America.

II. AREA OF STUDY.

Owing to the fact that succession is always either dependent upon, or modified by changes in conditions, a correct interpretation of this phenomenon depends largely upon accurate knowledge of the area under consideration.

1. *Location and General Character.*—The ponds which are the subject of this study lie in the sand area at the south end of Lake Michigan, within the corporate limits of the city of Gary, Ind. They may be reached from stations known as Pine, Buffington, or Clark Junction. This locality is characterized by a large series of sand ridges, for the most part nearly parallel with the lake shore (Map I.). Their average width is about 100 feet. They are separated by ponds which are somewhat narrower (Map II., p. 131). Most of these ponds are several miles long. They vary in depth during the spring high water, from a few inches to four or five feet. They describe an arc somewhat longer than the lake shore (Map I.), and are farthest from it about midway of their lengths.



MAP. I. This shows the arrangement of deposits at the south end of Lake Michigan. The general direction of the beach ridges is indicated and accordingly the general directions of the ponds. The number of such ponds and ridges cannot be indicated on a map of this scale. The former extent of Lake Chicago and subsequent lakes is indicated. The area in which the fish have been studied is represented by the larger rectangle. The black rectangle represents the area covered by Map. II.

Originally, there were probably a number of outlets to the system of ponds which were joined to one another by these outlets and through various low places in the sand ridges. In the area of our concentrated study there is an outlet (Map II.) which has served to connect all the younger ponds in an intimate fashion.

The building of sewers associated with the growth of northern Indiana towns (Whiting, East Chicago, Hammond and Gary) has drained large portions of the ponds, while roads and railroads have isolated other portions.

2. *Origin of the Ponds.*—During the final retreat of the North American ice sheet, its Lake Michigan lobe stood for a time with its southern end at the crest of the Valparaiso moraine which lies concentrically around the southern end of Lake Michigan. When the ice retreated from this position, water occupied the space between this lobe of the sheet and the moraine. This was Lake Chicago, the forerunner of Lake Michigan. After having stood respectively 60 feet, 40 feet and 20 feet above its present level, long enough to deposit conspicuous beaches, it took up a position at a 12-foot level. The waters appear to have fallen gradually from this level. At present one or two ridges and depressions similar to those found above the water on old Lake Chicago plain, are below the surface of the water along the shore at the south end of Lake Michigan. The retreat of the water has evidently exposed such ridges as fast as they were formed. This has left a *series of parallel ridges and ponds arranged in the order of their age—the oldest farthest from the lake, the youngest nearest the lake.*¹

These ponds are not all of the same size. The largest ones were selected for study and will be referred to in the paper by number as the entire series is counted inland from the lake shore. There are between seventy-five and ninety of these ponds or depressions between the lake shore and the 20-foot beach level. This is the maximum number. Map I. shows that as we pass in either direction from the area of study their number decreases.

¹ For a treatment of this subject, see articles cited in the bibliography but not specifically referred to here. Professor R. D. Salisbury tells me that there is no question concerning the relative age, from physiographic evidence alone.



MAP II. Shows the area of special study. The water is shown in black; the ridges and road and railroad grades, in white. The numbers 1, 5, 7, 14, etc., refer to the numbers of the ponds and ridges opposite which they are placed, as these ponds and ridges are counted from the lake shore. The dates associated with the indicated railroad grades refer to the approximate date of building of the grade, and probable damming of the long ponds where sluices were not maintained. The dotted lines are to bound the railroad grades; stippled areas represent recent filling.

Map II. shows the relations of the first twenty-four of these ponds. The recent changes of this smaller area are indicated on this map by the dates of the building of the various road and railroad grades.

III. THE DATA.

All methods of collecting have been employed. The dip net has been found most effective, but the drought of 1908 and draining by sewers have yielded crucial results in Ponds 1, the outlet, Pond 5a, 5c, 14a and 7b.

With the exception of *Amia calva*, the records are for adults, or for young where the pond is known to be *isolated*, and the presence of adults is therefore necessarily implied.

The record of *Ameiurus melas* in Pond 56 is based upon the presence of young and adults; identification of the adults depended upon identification of the young, because the adults were too badly macerated to make identification practicable.

1. *Distribution of the Species of Fish.*—The distribution of the fish in the various isolated parts of the ponds is of much importance. Turning to Map II., we note that the extension of the ponds to the east and west is not shown. Toward the east Ponds 1 to 17 become shallow near the Gary Steel Plant and are *not* connected with other bodies of water. Parts of Ponds 1 to 7 have been directly connected with the lake by the outlet (Map II.) until within the past few years. Excepting in the case of pond 7, other connections with the lake, to the northwest of the area shown on our map, have probably been closed for a much longer period. We may concern ourselves largely with the parts of the ponds to the east of the outlet, which have been isolated by railroad grades, and with their relation to the outlet.

Table I., taken with Map II., presents the exact data on the distribution of the fish in the various parts of the ponds. All fish nomenclature is after Forbes and Richardson, '08.

In Table I. we note first that the large-mouthed black bass, the sunfishes, the pumpkin seed, and the warmouth, are all confined to the outermost pond, or Pond 1. The passage from pond 1 to the outlet and to pond 5 was open until 1906. The study began in 1907. In the autumn of 1908 the drought reduced the water in the outlet to a minimum, but none of these species was

found there, though the passage between the outlet and pond I had been open two years before. Why have the fish vacated or avoided the outlet? One can only suggest a behavior reaction as the cause.

TABLE I.
DISTRIBUTION OF THE FISH.

The letters and numbers at the heads of the columns refer to the various isolated parts of ponds and, excepting o which refers to the outlet, may be located on Map II. The last column indicates the occurrence of fish in the older ponds of the series, which are not found on the map; the numbers refer to the number of the pond in which the fish were found. ? indicates an incomplete identification.

Common Name.	Scientific Name.	Ponds.									
		1	o	5a	5b	5c	7a	7b	14a	14b	
Large-mouthed black bass.....	<i>Micropterus salmoides</i>	*									
Blue gill.....	<i>Lepomis pallidus</i>	*									
Blue-spotted sun fish.....	<i>Lepomis cyanellus</i> ...	*									56
Pumpkin seed.....	<i>Eupomotis gibbosus</i> ...	*									
Warmouth bass....	<i>Chænobryttus gulosus</i>	*									
Yellow perch.....	<i>Perca flavescens</i>	*				*					
Chub sucker.....	<i>Erimyzon sucetta</i> ...	*	*		*	*		*			
Spotted bullhead...	<i>Ameiurus nebulosus</i> ...	*	*		*	*	*	*	?		
Tadpole cat.....	<i>Schilbeodes gyrimus</i> ...	*	*		*	*	*	*	?		
Pickrel.....	<i>Esox vermiculatus</i> ...	*	*	*	*	*	*	*	*		58
Mud minnow.....	<i>Umbra limi</i>	*	*	*	*	*	*	*	*		58
Golden shiner.....	<i>Abramis crysoleucas</i>		*	*	*	*	*	*	?		
Yellow bullhead....	<i>Ameiurus natalis</i>						*				
Black bullhead.....	<i>Ameiurus melas</i>						*	*	*		58
Dog fish.....	<i>Amia calva</i>									*	15

The perch is distributed in a still more peculiar way. It is found in Ponds 1 and 5c, but *not* in the outlet or in Ponds 5a and 5b. 5a and 5b were connected with the outlet until 1907 but 5c has probably been separated since 1851, when the L. S. & M. S. R. R. was built. I have no evidence that a sluice was ever maintained under this railroad in Pond 5. The perch is then distributed in such a way as to necessitate the conclusion, either that it was artificially introduced or that it was once in the outlet and in Pond 5a and 5b, because these make the only passage to Pond 5c where it now occurs.

The chub sucker is in all the ponds up to 7b, excepting 5a and 7a. The passage to, from, and through Pond 5a, and other points where the chub sucker occurs, was open until 1907 and the crucial collecting was done in 1908. It will be noted that

the distribution of the chub sucker in Ponds 7*a* and 7*b* is entirely similar to the distribution of the perch in Ponds 5*a* and *b* and 5*c*. The chub sucker is not in the part of the long Pond 7 which has been recently connected with the outlet.

It will be noted also that the tadpole cat and the spotted bull head have not been taken in 5*a*. The yellow bullhead has been taken from 7*a* but once, but we may expect that it is a resident of the locality. One would expect to find it in Ponds 5*b* and 5*c*.

With the exception of Ponds 14*a* and 14*b*, there are no noteworthy peculiarities. The study was begun in 14*a*. This was partially drained in the winter of 1908-9 and it was therefore necessary to turn attention to 14*b*. This was probably partially drained previous to 1892 by the East Chicago ship canal, but again renewed through a dam made by the building of the Wabash railroad grade between the point of draining and the part of the pond studied about 1892. This probably accounts for the presence of only a single species in Pond 14*b*. A single juvenile blue-spotted sunfish was found in Pond 56 which is directly connected with the Calumet River where it is common.

2. *Ecological Age of Ponds*.—The ecological age of the ponds is determined by an inspection of (a) the amount of bare bottom, (b) the amount and kind of vegetation, and (c) the amount of humus. It is a well-established fact that an entirely new pond (in the matter of recent separation from a lake, like Lake Michigan) has little vegetation and very little or no humus. Both vegetation and humus come only with age. Age-determination is so simple that no difficulty usually is experienced by one trained in plant ecology, in arranging a series of ponds in the order of their ecological age. In the matter of the kind of vegetation we have had the advice of Dr. H. C. Cowles.

Pond 1 is the youngest, because it has the kind of vegetation that grows in young ponds, more bare sand bottom, least humus, and least vegetation. For similar reasons Ponds 5*b* and 5*c* stand second in the matter of age. Because of human interference, which has kept the vegetation down in Pond 5*c*, it is probably ecologically younger than 5*b*. The outlet is probably intermediate between 5 and 7. Ponds 7*a* and 7*b* stand next, but without any difference as far as one can see.

From the standpoint of bare bottom and humus Pond 5a is very much advanced. Being located near the outlet, it has become filled with decaying vegetation and a floating bog, now destroyed, indicated an advanced stage comparable with 14. It differs from 14 in possessing qualitatively "younger" vegetation and some other characters of youth. The differences between 14a and 14b have already been discussed.

In Table II. the ponds or parts of ponds are arranged in order of ecological age and the distribution of fish is shown.

TABLE II.

DISTRIBUTION OF FISH: PONDS ARRANGED ACCORDING TO ECOLOGICAL AGE.

Common Name.	Scientific Name.	Ponds.							
		1	5b 5c	7a 7b	5a	14a	14b	5b 58	52
Large-mouthed black bass.....	<i>Micropterus salmoides</i> ..	*							
Blue gill.....	<i>Lepomis pallidus</i>	*							
Blue-spotted sunfish....	<i>Lepomis cyanellus</i>	*						*	
Pumpkin seed.....	<i>Eupomotis gibbosus</i>	*							
Warmouth bass.....	<i>Chænobryttus gulosus</i> ...	*							
Yellow perch.....	<i>Perca flavescens</i>	*	*						
Chub sucker.....	<i>Erimyzon sucetta</i>	*	*	*					
Spotted bullhead.....	<i>Ameiurus nebulosus</i>	*	*	*					
Pickereel.....	<i>Esox vermiculatus</i>	*	*	*	*	*		*	
Mud minnow.....	<i>Umbra limi</i>	*	*	*	*	*		*	
Golden shiner.....	<i>Atramis crysoleucas</i>		*	*	*	*			
Yellow bullhead.....	<i>Ameiurus natalis</i>			*					
Black bullhead.....	<i>Ameiurus melas</i>			*	*	*	*	*?	
Dogfish.....	<i>Amia calva</i> (juvenile)...								*

When the ponds are arranged according to ecological age, there is a noticeable symmetry in the distribution of the fish, and we are at once interested in its meaning.

IV. INTERPRETATION AND DISCUSSION OF THE DATA.

We have noted from the tables and discussion of tables that the present distribution of the fish is correlated with (A) the age of the ponds (Table II.) and (B) the length of time that channels have been open (Table I.).

It is a well-known fact that ponds fill with plant detritus. With the filling of ponds, the conditions change progressively in a definite direction. In a pond which remains in the same

general physiographic relations during a considerable period of time, there is a succession of conditions due to the accumulation of detritus just as there is a succession of conditions in a stream due to physiographic changes.

Since the channels of communication between the different ponds have been open until recently, the present arrangement of the species of fish is very probably a *behavior adjustment* to the changed and changing conditions just so far as barriers have permitted.

We see from the arrangement and mode of origin of the ponds that our oldest pond—number 14, Map I., and Fig. 1, was once in the same relation to the lake as Pond 1 is now. At such a time it was in a condition similar to that of the present Pond 1. Ponds 5 and 7 are intermediate in conditions between Ponds 1 and 14. We have the same general basis for the discussion of ecological succession as in the streams. The changes in these ponds have depended mainly upon physiographic stability within each pond, rather than upon physiographic changes, and have been due to the *action of the organisms present on their own environment*.¹ This is true because after a given pond is once separated from the lake (Fig. 1) the changes due to the organisms go on without regard to further separation and the lowering of the lake level. Evidently the level of the water has remained much the same in the ponds after their separation from the lake proper regardless of the lowering of the lake level (Fig. 1).

The method of deducing succession herein employed is similar to that used in the case of the streams. The easily observable fact that animals occupying similar conditions are ecologically similar (*i. e.*, similar in habits and some main features of their physiology of external relations) is used as a starting point, and the conclusions drawn are to the effect that when the older habitat was in the stage of a younger habitat, it was occupied by *fishes ecologically similar to those now in the younger habitat*. Whether they were the same or different species is often of little importance to ecological succession. With this simple explanation as a background, and with the use of Figure 1, we will

¹ The changes which are caused by the filling of the pond with plant material are physiographic, but the biological aspect is the more important, and we may discuss the changes as caused by biological forces.

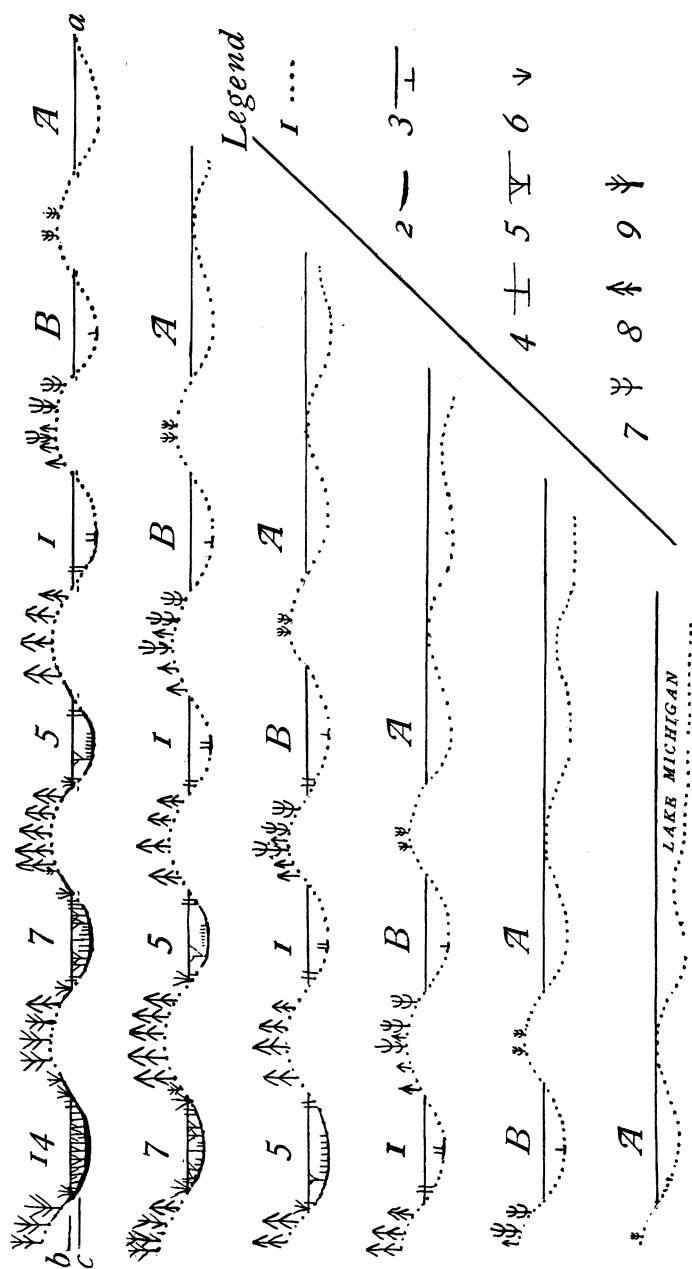


FIG. 1. Diagram showing the relation of the horizontal and vertical series of pond stages. The horizontal series at the top represents the present ponds with the intermediate ones omitted and hypothetical stages A and B added. The line a-b represents the ground water level; the line a-c, indicated by occasional dashes, the level of the lake. When read from bottom to top the entire figure represents the history of the area; showing the addition of ponds near the lake shore and the aging of the others. The left-hand vertical series (A, B, 1, 5, 7, 14,) represents the history of the present Pond 14, and is used as the basis for the discussion of succession. The legend is as follows: (1) sandy bottom, (2) humus, (3) plants that do not reach the surface, (4) bulrushes, (5) aquatic plants which reach to the surface of the water, (6) shrubs, (7) cottonwoods, (8) pines, (9) oaks.

state, as well as practicable, the succession in these ponds with particular reference to fish.

1. *Statement of Ecological Succession.*—A statement of succession can be best made in the form of a history of Pond 14 (Fig. 1). From our knowledge of the origin of the ponds and their present topography, it is reasonably certain that there was a time when Pond 14 was more closely associated with the lake than Pond 1 is at present (Fig. 1, hypothetical stage B). At such a time Pond 14 contained less vegetation than we now find in Pond 1. For a knowledge of the ecological character of the fish which inhabit such ponds, we have collected from a pond of the same origin as those made the subject of the present study. This one has maintained a close connection with Lake Michigan and receives the waves of the lake during the spring and winter storms. It flows into the lake during every highwater period. This pond is at Beach Station, four miles north of Waukegan, Ill. Near its outer end it presents a clear bottom of sand and gravel, little vegetation and no humus. In this outer portion we have collected the pike (*Esox lucius*), which prefers clear, clean, cool water (Forbes and Richardson, '08); the red horse (*Moxostoma aureolum*), which dies quickly in the aquarium if the water is the least impure and succumbs to impure conditions in its native waters (Forbes and Richardson, '08); *Notropis cayuga*, common in Cayuga Lake and the lower course of its tributaries (Reed and Wright, '09). As compared with Illinois waters, these streams would be counted clear. We also found *Notropis cornutus*, which shows a marked preference for clear waters (Forbes and Richardson, '08).

When Pond 14 was in a very early stage (hypothetical stage B, Fig. 1) it must have been occupied by fishes which were ecologically similar to the red horse, the pike, the cayuga minnow, and the common shiner. This is a community of species which may be characterized as requiring clear, clean waters, clean bare bottom (especially during the breeding season), and little vegetation. Such fishes may be designated as *pioneer ecological types*. To this group might be added such fishes as the common perch, which is hardy and lives in a wide range of conditions.

Following the history of Pond 14 further, we note that as the

vegetation grew, humus accumulated in the deeper parts, and forms ecologically similar to the black bass, the blue gill, the pumpkinseed, and the white crappie (*Pomoxis annularis*) which is widely distributed (Forbes and Richardson, '08), but which Meek and Hildebrand ('10) record only from streams and ponds which are ecologically young, must have made their appearance, if any such fishes were available. All but one of these species were taken from the pond at Beach but chiefly from the older parts. They were not clearly separated from the other species, but conditions were graded and no barriers present. We would expect the absence of some of the pioneer ecological types, such as the pike and the red horse, from such a community.

When the conditions in Pond 14 which made the habitat suitable for the last mentioned fish community had progressed a little further, *all the organisms present must have sufficiently affected the habitat to render the continued existence of some of the pioneer ecological types impossible, and at the same time prepared the way for new ecological types*, such as the blue spotted sunfish, the little pickerel, the chub sucker, the warmouth bass, the spotted bullhead and tucked away in the mud of the deeper portions a few fishes ecologically similar to mud minnows and tadpole cats.

This is the condition of our Pond 1 at present—a shallow pond with considerable accumulations of humus in the deeper parts, and much of its bottom covered with *Chara* and other plants. In this connection it should be noted that Meek and Hildebrand ('10) record the crappie and top minnow (1900) from Pond 1 (Map II.), but they are no longer found there.

It should be remembered that the parts of a pond which are so situated as to most easily allow the accumulation of plant detritus will be first to become unfavorable to pioneer fishes, while the parts which are swept clean by wave action remain in a good condition for a much longer period of time. Stages in pond development such as the present Pond 1 are the most complex of all, and are more like the larger lakes. Such stages are in a condition to support a greater diversity of ecological types than the later stages. While still retaining a part of its pioneer fishes, Pond 1 supports the forms which belong to other older conditions (mud minnow and tadpole cat).

Up to such a stage, Pond 14 must have become from the first more and more favorable to diversity of ecological types, and accordingly possessed at such a time its greatest number of species of fish. When Pond 14 was at a stage comparable to the present Pond 1, the fish community present and all the other organisms associated with it, so acted on their environment (just as they are acting on their environment in Pond 1 at present) as to make the habitat less favorable to the fish of the earlier pond stages, and more and more favorable for those dependent upon and tolerating dense vegetation, absence of bare bottom, and lower oxygen content. As a result of this action of the biota on its environment, the fishes of ecological constitution similar to that of the sunfishes and basses now present in Pond 1, disappeared either by emigration or death. In the absence of these, and in the more favorable conditions of competition and denser vegetation, fish, such as the golden shiner, were able to find a suitable habitat. At such a stage Pond 14 possessed a fish community of the ecological character of that now found in Pond 5c. Here the pioneer element is reduced to a single species, the perch, which is very hardy (Hankinson, '07).

The same process continued and caused the disappearance of the perch and like ecological types. A fish community ecologically like that now in Pond 5b (Table I., column 3) then existed. The absence of the perch in 5b and its presence in 5c may be explained, judging from the general habits of the perch (Forbes and Richardson, '08), by the fact that neither pond appears to be favorable for perch and they have been able to move out of Pond 5b, but not out of Pond 5c. An experimental comparison of the behavior of perch from Pond 5c and other perch habitats would have an important bearing on our problem.

The fish community of Pond 5b is made up of the chub sucker and the golden shiner, which are abundant, the spotted bullhead, the tadpole cat and the mud minnow. The spotted bullhead is the only one known to use bare bottom for nesting. There is only a little bare bottom in Pond 5b. The spotted bullhead usually builds its nest under cover (Eycleshymer, '01).

When such a fish community occupied Pond 14, the biota present gradually changed its own environmental conditions as

the former stages had done. The nature of the changes are evident now when we can compare Ponds 5*c* and 5*b* with Ponds 7*a* and 7*b*. In ponds 7*a* and 7*b* we find water lilies and bladderwort in abundance. These are barely present in 5*b* and 5*c*. Ponds 7*a* and 7*b* have much less bare bottom than 5*b* and 5*c*.



FIG. 2. Shows Pond 1 at the extreme low water of the drought of 1908. In the spring the old boat is usually covered with water. In the foreground a large area of bare sand bottom is shown; to the right a few rushes and sedges. The absence of shrubs near the water's edge should be noted.

This is present in favorable situations very near the water's edge.

The fish community of 7*b* is made up of the same species as the community of 5*b*, with the addition of the black bullhead. 7*a* lacks the chub sucker, and here as has been noted the chub sucker bears the same relation to the two parts of Pond 7 as the perch does to Ponds 5*b* and 5*c*. It is evident that it moved out of the pond from which a channel of exit has been open.

The first step in the transformation of the fish community of Pond 14, which was ecologically similar to the present 7*b*, into the next later stage, was the loss of such ecological types as

the chub sucker and the addition of such as the black bullhead. The latter is a well-known "mud-lover" which inhabits the oldest stages of pond succession. As the conditions which organisms produced increased in intensity in the directions indicated, the species ecologically similar to the tadpole cat and the spotted bullhead disappeared, and with them probably the golden shiner also. With the loss of these we have the fish community which was in Pond 14a before draining. It is illustrated by Pond 5a also, in which the plant and animal detritus has collected



FIG. 3. Showing Pond 14 at moderate low water. In contrast with 1, we see that it is choked with vegetation and the margin occupied by shrubs and bulrushes, etc.

because it is located at the outlet where the channel becomes shallower and narrower. Ecological types, such as the pickerel, the black bullhead, and the mud minnow make up this community in Pond 14. They usually continue until the pond becomes temporary when they are destroyed by drying.

2. *The Future of the Pond.*—Ecology is one of the few biological sciences in which prediction is possible. I shall venture to predict the fate, in a state of nature, of a pond like Pond 14a *was* at the

point where the study was first begun, before the draining took place.

Had Pond 14a not been disturbed by man, it would have continued to fill with humus. Its center would have come to be occupied by the cat tails, bulrushes, *Proserpinaca*, and *Equisetum*, all of which invade from the sides. When such a stage was reached it would be subject to almost complete drying in extreme droughts and the fish would be eliminated in the order of their ability to withstand draught, and in relation to accidents of distribution in parts of the pond drying to various degrees.

In September, 1908, we were able to obtain evidence on this point from some of the older ponds. A group of black bullheads, grass pickerel and mud minnows were found in the lowest part of one of the sections of pond 58. The pickerel were dead and badly decayed. The bullheads were dead and just beginning to decay, but the mudminnows, fully a bushel of them, were still alive although without water. This lot included some of the largest individuals collected.

When Pond 14 reached such a stage, its fish content would become very problematical, dependent upon the distribution of the different species with respect to deeper and shallower parts of the pond, and the length of the drought, as related to the resistance of the different species. Evidence for this is seen in Pond 14b, where *Ameiurus melas* is the only species present since a probable partial drying of the pond.

Indeed, we may carry the prediction one step farther. When such a pond becomes of this sort the plants that take hold of it are the grasses, sedges, etc., which fill the soil with roots, and form hummocks. If accessible to them, such ponds become the breeding place of the dog fish. During the drought of 1908 I found a school of half grown dog fish in such a pond, which answered the description of the favorite breeding place of the dog fish as given by Reighard ('02). Such a stage as this will be followed by the invasion of shrubs and the final destruction of the pond as an aquatic habitat.

We have in ponds a progressive change in the conditions and a progressive change in the ecological and physiological character of the fish communities, and a succession or evolution of fish

communities through emigration, death, immigration, and the modification of *mores* by external stimuli.

V. ECOLOGICAL SUCCESSION AND SUCCESSION OF SPECIES.

The difference between ecological and geological succession were suggested in my preceding paper. We noted that ecological succession deals with the succession of *ecological types*. We noted also that geological succession is due, in the main, to the death of a given set of *species* and the evolution of new ones throughout geological time. While this is true of the broader aspects, in the more detailed cases and especially in dealing with recent post-glacial fossils, the palæontologist often encounters a vertical succession of fossils which have been left behind by the migrations of a succession of species over the locality of fossilization (Warming, '09, p. 362, Adams, '05 and '09, Sharff, '07, esp. Chap. IX. and citations). Palæontologists may also encounter vertical succession of fossils in situations where such succession as we have been describing has taken place.

1. *Vertical Succession of Fossils*.—Steenstrup ('41) found from the study of fossils in moors that one kind of vegetation succeeded another. Various other workers (Andersson, '97) have found similar arrangements. In the case before us the fossilization of species would give a vertical succession of fossils.

Turning again to the diagram, we note that the skeletal parts of any fish in the earliest stages indicated by hypothetical stage B might have been preserved as fossils. The accumulations of humus which lead up to stage 1 would have covered the fossils of stage B, the fish of stage B would be present, if at all, as fossils at the bottom of the pond.

Likewise, the accumulations of humus which led to stage 5 covered those skeletal parts of the fish of stage 1, and the fish of stage 1 should be found as fossils overlying those of stage B and underlying those of stage 5. Again, the accumulations of humus which led up to stage 7 covered fossils which were present and added at stage 5, and the fish preserved as fossils from stage 5 would lie above all those preserved as fossils from the younger stages and below those of stage 7. Fossils from stage 14 and the intermediate stages would lie at the top of the series and above those of stage 7.

However, no such arrangement of fossils has been found in these ponds. No attempt to ascertain whether or not they are present has been made.

2. *Relation to Climatic Changes.*—As has been indicated, succession is due to changes in conditions which make it impossible for a given group of organisms to continue to live at a certain locality. Accordingly, such a group gradually disappears and is gradually succeeded by a group which is adapted to the new conditions.

The changes in conditions referred to are climatic or physiographic changes, and others independent of physiography and climate. The last type of change is usually due to the action of the organisms themselves. These three forces may act separately or together. The latter is probably the more common. In case the changes are climatic, both the ecological succession and the succession of species over a locality might be partly due to migration of a succession of species. Narthorst ('70, fide Warming, '09, p. 362) found that the oldest fossils underlying moors are of arctic tundra plants. In post-glacial dispersal arctic-tundra plants and animals were succeeded by conifers and associated animals, and by deciduous trees and associated animals (Adams, '05).

3. *Relation of Horizontal Series and Vertical Succession.*—Cowles ('01) pointed out the fact that there is frequently a horizontal series of successional stages (habitats of different ages) associated with continuous physiographic processes, such as the deposition of sand along shores. The diagram (Fig. 1) illustrates both the horizontal and vertical series of conditions with which we have been dealing. Cowles ('01) further pointed out that the horizontal series of plant communities must bear a close ecological resemblance or be practically identical with the vertical series of past plant communities which have succeeded one another over a given locality in the older part of the horizontal series. He pointed out further that the horizontal series may be taken as an index of what the vertical series has been. He would except the first stages of plant communities which occupied a locality at the close of the ice age and which as has been stated, are arctic plants. These arctic plants, however, must have affected

the soil or pond bottom in much the same way as the pioneer plants of the present climate would affect them. The differences resulting from the change of climate are then, those of detail rather than of principle.

4. *The Relation of Ecological Succession to Species of Fish.*—If fish were found fossil in the bottom of Pond 14, in the order which we have indicated, one might conclude at once that it constituted a proof of ecological succession. This seems to have been the general impression of zoölogists who have heard the presentation of these data. The question has been asked, "Do you find fossil in 14 all the fish which you mention as occurring in succession there?" My answer to the effect that no such fact has been discovered seems to have been regarded as constituting a refutation of the entire statement of ecological succession.

If fish were found fossil in the order described above, and the species and order of species, the same as now found in the horizontal series of ponds, we would have some important data bearing on succession, migration, and other matters of interest to be discussed presently, but this would yield *no crucial evidence for or against ecological succession*. Ecological succession is based upon physiology, habits, behavior, mode of life, and the like, which I have proposed to call *mores* (opposed to the term form). Unless the *mores* of the morphological species found fossil were the same as the *mores* of the same morphological species at present, they would have no weight in the matter, and it would be impossible to ascertain *mores* from fossils if such fossils were found.

If the same one or more species were found fossil in each and all of the vertical stages of a pond like 14, the evidence would not refute the proposition of ecological succession because the physiological characters of the individuals of a given species living in the early stages could have been very different from those of individuals living in later stages, without the differences being shown in the preservable skeletal structure. Furthermore the modifiability of animal behavior seems well established. The same species of plant may remain in a number of different pond stages. Such plants show suitable functional responses manifested by different growth-forms in different stages.

The proof of ecological succession must rest on the results of experimental work on the animals of the different stages of such a horizontal series. *It matters not from the point of view of ecological succession what the forms are, so long as the mores are different in the different stages of the horizontal series, and the character of the mores is correlated with the environmental conditions.* When such differences and relations are found, ecological succession is essentially established. It is of course recognized that within rather uncertain limits the *mores* of a morphological species remain, in a general way, the same throughout its geographic range. This kind of reasoning must be pursued with caution. When applied in detail or to "common" species which are wide ranging, it is not at all trustworthy. If, for example, an examination of the deposits in the bottom of a pond, such as Pond 14, showed the presence of a fish which now habitually inhabits the *youngest stages* of pond succession, let it be a more northern, or the same species as those in the horizontal series under consideration, it would constitute some evidence for ecological succession which could be further checked by the study of the modifiability of the *mores* of that species at present. However, in no case can this kind of evidence be crucial.

Furthermore, the conditions such as were in primaeval Pond 14 could have been reached by a pond like Pond 1 in a few hundreds of years. In a pond with a soil more suitable than sand for the growth of aquatic plants, these changes could take place within the life time of the builder of such a pond (Knauthe, '07, p. 575).

VI. GENERAL DISCUSSION.

We noted in the preceding paper that physiographic analysis is a method. Here we have employed another method which, while not physiographic, is similar in principle, since it deals with succession over a given locality. The cause of this succession is biological and the biological interest is proportionately greater.

We have here the same attempt to discover something of the physiological character of the organism as a whole, and to classify organisms on the basis of the conditions in which they are most nearly in physiological equilibrium. Again, the *mores* of the fish of pond stages in other parts of the world are probably similar if the ponds are similar.

However, a legitimate question at this point would be: "What is the value of all this reconstruction and these complicated conceptions to biological science and the analysis of the organism?" Indeed, this is a question which we have asked ourselves repeatedly while working through the necessary plant data and all the scattered unorganized literature with which the investigator in this line must deal. The question has always been answered in a manner satisfactory to us because whatever value the papers on the ponds of the south end of Lake Michigan and other similar papers may possess, is due to the conception of pond succession acquired from the plant ecologists. Had I not acquired this knowledge I would have done as others have done—worked this excellent area over without seeing anything in it. The problems that have arisen in connection with this work have given a fresh point of view and a motive for investigation which has repaid the effort.

In connection with problems and motive for their solution, it should be noted that this is one of the most important things which the plant ecologists regard as of value in the conception of succession. Cowles, who has done more to stimulate work on succession and the use of physiographic method than any other American ecologist, regards functional response of plants (determined by watching plants and experimenting on plants) as much more fundamental than succession. This appears to be generally true of plant ecologists. Warming, who has been a great leader in ecology, emphasizes the physiological side.

We have, then, among the workers and originators of the use of this principle, a condition with respect to its place in biology which is quite different from what one would expect from simply noting what has been the dominant thing in their work. The relation of the historical and genetic side of ecology to more fundamental physiological and ecological problems, is similar to that of the historical and phylogenetic side of evolution, to the problems of biology and the motives for investigation. When Darwin framed the idea of evolution into a logic which was not refutable by academic attack, the facts of biology took shape, arranged themselves into orderly relations to each other. This made possible methods of work which were new, opened up new

problems, the attempt at the solution of which has made modern biology what it is.

If we assume the attitude that nothing can be done in the organization of natural history materials into a science, we are closing the question to investigation, much as the idea of special creation closed other lines of biological investigation. Still an occasional biologist appears to take this point of view.

Aside from the general questions which we have been discussing, there are many practical applications of pond succession to the study of behavior and to the economic and quantitative side of biology. These we will discuss in a succeeding paper under the head of the causes of succession in ponds.

VII. SUMMARY.

1. There is a series of ponds at the south end of Lake Michigan arranged in the order of their age; age is determined by the physiographic history; by the relative amount of humus and bare bottom, and by the quality and quantity of vegetation.

2. Species of fish are arranged in these ponds in an orderly fashion; the order is related to the age of the ponds.

3. The ponds of different ages represent stages in the history of older ponds.

4. The horizontal series of fish communities is ecologically representative of the succession of fish communities within the older ponds.

5. The method employed here is similar to physiographic analysis; the motives and possible results are similar but more strictly biological, because the causes of the succession are the organisms themselves.

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